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Technical Report 32-1359

*A Mathematical Model of the Effect of a Predator
on Species Diversity*

*J. N. Yang
C. R. Weston*

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**JET PROPULSION LABORATORY
CALIFORNIA INSTITUTE OF TECHNOLOGY
PASADENA, CALIFORNIA**

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Preface

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Contents

I. Introduction	1
II. Operation of the Chemostat	1
III. Assumptions and Mathematics Governing the Growth Model	2
A. Governing Differential Equations	2
B. Specific Growth Rate	3
IV. Numerical Analysis	4
A. Numerical Solution of Dynamic Response	4
B. Steady-State Solution	5
C. Stability Criterion of the Steady State	6
V. Numerical Results	9
A. Effect of B_1 , B_2 , and B_y	9
B. Change of Dilution Rate	9
C. Changed Input Substrate Concentration	11
VI. Discussion	11
A. The Chemostat Model	13
B. Formulation of the P Function	14
C. The Formulation of Growth Rate	14
D. Deterministic vs Stochastic Solutions	14
Nomenclature	15
References	16

Figures

1. Relationship between specific growth rate μ and resource concentration s	3
2. Illustration of the effect of M and σ on the P function	5
3. Equilibrium level of species X_1 and its limiting resource S when there is no competition for the resource and no predation	8
4. Unsuccessful competition of species X_2 for resource S in the absence of predation	8
5. Increased level of resource S when predator Y preys upon X_1 (three-variable system)	8

Contents (contd)

Figures (contd)

6. Coexistence steady state of X_2 and X_1 when X_1 is preyed upon by Y (four-variable system)	9
7. Effect of level of endogenous metabolism B on three-variable system when $B = 0.001$	9
8. Effect of level of endogenous metabolism B on three-variable system when $B = 0.0$	10
9. Effect of dilution rate D on three-variable system when $D = 0.07$	10
10. Effect of dilution rate D on four-variable system at $D = 0.07$	10
11. Effect of dilution rate D on three-variable system when $D = 0.15$	11
12. Effect of dilution rate D on four-variable system. Note that X_2 is unsuccessful at $D = 0.15 \text{ h}^{-1}$, reverting to three-variable system	11
13. Effect of input resource concentration s_r on three-variable system ($s_r = 150 \text{ mg/l}$)	11
14. Effect of input resource concentration s_r on four-variable system (note that X_2 is unsuccessful at $s_r = 150 \text{ mg/l}$, reverting to three-variable system)	12
15. Effect of input resource concentration s_r on three-variable system ($s_r = 250 \text{ mg/l}$)	13
16. Effect of input resource concentration s_r on four-variable system ($s_r = 250 \text{ mg/l}$)	13

Abstract

The presence of two species in the same environment with a common limiting resource is paradoxical if competition for the limiting resource is the only consideration: One or the other of the species must be eliminated. This analysis shows that a normally unsuccessful competitor for the limiting resource *may* persist when there is a predator on the otherwise successful species. The modified assumption and different parametric values which are considered do not alter this generalization. The working model is of bacteria growing in a chemostat; however, there is no reason to assume the resultant conclusions are restricted to a bacterial system, an experimental situation, or terrestrial organisms.

A Mathematical Model of the Effect of a Predator on Species Diversity

I. Introduction

In sampling alien soils with life-detection instrumentation, it is a basic assumption that the biological phenomena which apply on earth are applicable universally. One of the striking features of terrestrial soils is the great diversity of microbial species present, many of which have overlapping nutritional requirements. Even a partial overlap in nutrient needs between two microbes in a given environment challenges the competitive exclusion principle, an ecological generalization that no two species can coexist indefinitely when they require a common limiting resource.

Drawing examples from higher organisms, Paine (Ref. 1) suggested that predators play an important role in maintaining species diversity. He reasoned that since predators reduce the number of individual prey organisms in a population to the level where they cannot fully exploit their potential resources, resources never limit population growth in the presence of the predators. The further implication is that another species which would have been excluded in competition for the resource may enter the environment and exist on an unexploited residue of resource.

The predator's postulated role of controlling the amount of species diversity is obviously of general theoretical

interest. Thus, we have tried to determine its validity based on more explicit assumptions than those expressed by Paine or Spight (Ref. 2) in his subsequent critical paper. Our working model consists of bacteria growing in a chemostat. We believe, however, that basically the model is restricted to neither bacterial systems nor experimental situations. Some limitations of the model and some possible modifications are discussed in this report.

II. Operation of the Chemostat

The chemostat is a constant-volume culture vessel wherein the specific growth rate μ is regulated by the rate at which fresh nutrient S is introduced. The variable D is the dilution rate, or the ratio of the rate of nutrient input f to the culture volume V ; i.e., $D = f/V$. The culture volume is maintained constant by removing fluid (including a proportionate number of cells) at the same rate as nutrient solution is introduced. Hence, the bacterial population x is regulated by the difference between the population growth and removal,

$$\frac{dx}{dt} = \mu x - Dx \quad (1)$$

At steady-state equilibrium, the specific growth rate is the same as the rate of dilution:

$$\frac{dx}{dt} = 0, \quad \mu = D \quad (2)$$

The basic principles of chemostat culture and the steady-state mathematics were developed by Herbert, Elsworth, and Telling (Ref. 3).

A bacterial population and the nutrient concentration in a chemostat will come to a unique equilibrium for a given dilution rate and nutrient input. The principal exception occurs when the dilution rate exceeds the maximum regeneration rate of the organisms. On the other hand, whenever two bacteria which have the common resource are added together in the chemostat, they will not come to a steady-state equilibrium. One or the other of the species will be displaced in competition for the limiting nutrient (see, for example, Ref. 4); thus, in time, the culture reverts to the steady state with a single consumer. An analogous competitive situation with higher organisms (beetles) has been demonstrated by Park (Ref. 5).

It is the purpose of this study to determine what happens to the steady-state concentration of nutrient in the chemostat when a predator, such as an amoeba, is introduced, which has the normally successful bacterial competitor as its sole resource. In particular, we have sought conditions under which an increase in nutrient would result, permitting the normally unsuccessful bacterial species to coexist.

In the subsequent discussion, frequent reference is made to population level (size, concentration, number). It should be understood that all calculations are based on weight (in milligrams) per unit volume (in liters), where weight is the aggregate weight of the population (biomass). The discussion is qualitatively accurate for numbers of individuals, although a rigorous discussion would account for the distribution of individual size and for changes of mean size with age of culture.

III. Assumptions and Mathematics Governing the Growth Model

The analysis of the interactions of the predator and consumer populations and their resources can be conveniently considered in two parts: first, the development of a basic set of differential equations which describe

the interactions with the specific growth rates (treated as undefined variables); second, a description of the specific growth rates as they are affected by population density and nutrient concentration.

A. Governing Differential Equations

Let s_r be the initial concentration of the limiting nutrient S in the inflowing medium, and s the concentration of this nutrient in the chemostat environment. Let x_1 be the concentration of bacterium X_1 with the specific growth rate μ_1 , and x_2 the concentration of bacterium X_2 with the specific growth rate μ_2 . Both X_1 and X_2 have the common requirement of resource S . Let y be the concentration of the predator Y , which has bacterium X_1 as its limiting resource, with μ_y the specific growth rate of Y in the culture.

During a very small time interval Δt , the population x_1 gives rise to $x_1\mu_1\Delta t$ new cells per unit volume, while an amount of X_1 proportional to x_1 , D , and Δt is removed from the culture vessel; i.e., $-x_1 D\Delta t$. Also, another amount of X_1 is consumed by its predator Y . The conversion of x_1 to y_1 occurs with some yield factor c_y . The remaining fraction of x_1 is oxidized into small molecular waste products to serve energy metabolism. Thus, the change of x_1 as a result of predation during the interval Δt is $(-\mu_y y/c_y) \Delta t$; hence, the variation of x_1 during the interval Δt is

$$\Delta x_1 = \mu_1 x_1 \Delta t - D x_1 \Delta t - \frac{\mu_y y}{c_y} \Delta t \quad (3)$$

Similarly, one can obtain the variations of x_2 and y as follows:

$$\Delta x_2 = \mu_2 x_2 \Delta t - D x_2 \Delta t \quad (4)$$

$$\Delta y = \mu_y y \Delta t - D y \Delta t \quad (5)$$

During the same interval, a concentration s_r of the limiting nutrient substrate enters the culture vessel at a specific dilution rate, while a concentration of s leaves at the same rate. Furthermore, a certain amount of nutrient is consumed by X_1 and X_2 . Hence, the total change of the limiting nutrient is

$$\Delta s = D s_r \Delta t - D s \Delta t - \frac{\mu_1 x_1}{c_1} \Delta t - \frac{\mu_2 x_2}{c_2} \Delta t \quad (6)$$

where c_1 and c_2 represent the yield factors of s to x_1 and s to x_2 , respectively.

Dividing both sides of Eqs. (3-6) by Δt and taking the limit as Δt approaches zero, a system of differential equations can be obtained as follows:

$$\frac{dx_1}{dt} = \mu_1 x_1 - D x_1 - \frac{\mu_2 y}{c_y} \quad (7)$$

$$\frac{dx_2}{dt} = \mu_2 x_2 - D x_2 \quad (8)$$

$$\frac{dy}{dt} = \mu_y y - D y \quad (9)$$

$$\frac{ds}{dt} = D s_r - D s - \frac{\mu_1 x_1}{c_1} - \frac{\mu_2 x_2}{c_2} \quad (10)$$

B. Specific Growth Rate

Any realistic model of population growth must provide that the growth rate of the organisms be a function of population size and nutrient concentration. At the extremes, failure to account for population size would allow the population size to become greater than the physical environment, while neglect of nutrient concentration would allow growth to occur with no nutrients present. These limitations in some growth models have been examined by Smith (Ref. 6).

The function describing the relationship between growth rate and nutrient concentration should have such properties that (1) no growth takes place without nutrient, and (2) the rate approaches a maximum value at elevated concentrations. The need for item (1) is self-evident; item (2) expresses the experimental observation that it is possible to provide resources at concentrations in excess of the organisms' needs—where no increase in growth rate would result from added nutrients.

The relation between growth rate and population size must be one where growth is strongly inhibited as population density approaches some maximum, but affected negligibly when there are few organisms.

Monod (Ref. 7) showed that the specific growth rate for bacteria is an increasing function of the concentration of the nutrient S of the form

$$\mu = \mu_m \frac{s}{k + s}$$

where μ_m is the maximum value of μ at saturation level of the nutrient substrate and k an *affinity* constant. Equation (11) has been successfully applied to scores of experiments. Figure 1 illustrates the nature of this function and the relation of k to the maximum growth rate.

This formulation satisfies the conditions already discussed. Additionally, the constant k expresses differing abilities of organisms to utilize nutrients at low concentrations. This last quality is the prime consideration governing survival of one or the other species in pure competition; that is, it will determine the interaction between two organisms based solely on their mutual need for a common resource, without any other ecological factor (such as predation).

It is well recognized that continued growth, even with an excess of nutrients, is limited at elevated population densities. The mechanism for this self-inhibition of the population is seldom known, but in a bacterial culture it is usually attributed to accumulation of metabolic byproducts.

In this study, the growth rate is considered not only as a function of s but of population density; thus

$$\mu_1 = \mu_{m1} \frac{s}{k_1 + s} P(x_1; M_1, \sigma_1) \quad (12)$$

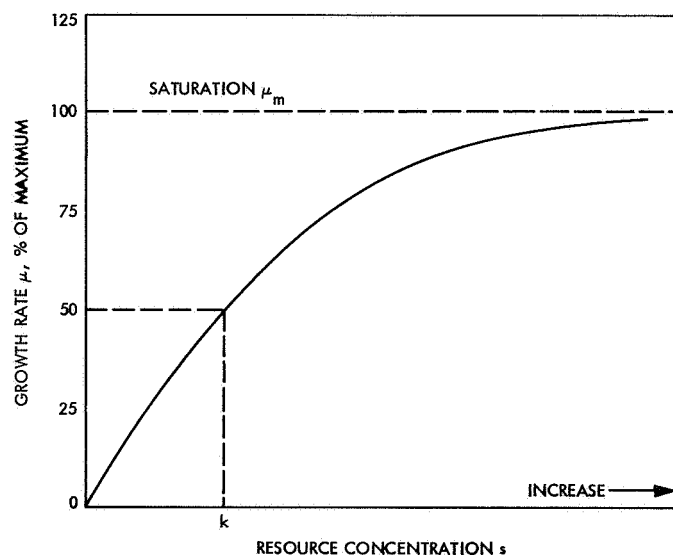


Fig. 1. Relationship between specific growth rate μ and resource concentration s

in which μ_{m1} is the maximum value of μ for x_1 , and

$$P(x_1; M_1, \sigma_1) = 1 - \phi\left(\frac{x_1 - M_1}{\sigma_1}\right) + \phi\left(\frac{-M_1}{\sigma_1}\right) \quad (13)$$

$$\phi\left(\frac{x_1 - M_1}{\sigma_1}\right) = \frac{1}{(2\pi)^{1/2}} \int_{-\infty}^{(x_1 - M_1)/\sigma_1} \exp\left(-\frac{\xi^2}{2}\right) d\xi \quad (14)$$

with $\phi(x_1)$ being the Gaussian (or Normal) distribution function, and mean value M_1 and standard deviation σ_1 being constant parameters associated with a specific organism. The limitations of this formulation are discussed later.

The function $P(x_1; M_1, \sigma_1)$ has the property that it approaches one at low values of x_1 and tends toward zero at high values of x_1 . The mean value M_1 and standard deviation σ_1 can be adjusted so that $P(x_1; M_1, \sigma_1)$ can approximate the experimental result for a specific organism. More precisely, M_1 represents the population concentration at which $\phi[(x_1 - M_1)/\sigma_1] = 0.5$ for $x_1 = M_1$, while σ_1 represents the bandwidth over which $\phi[(x_1 - M_1)/\sigma_1]$ decreases from near one to near zero (called dispersion). The magnitude of σ_1 indicates how fast $P(x_1; M_1, \sigma_1)$ decreases from near one to near zero. The following is a tabulation of the Gaussian distribution function $\phi[(x_1 - M_1)/\sigma_1]$ as a function of x_1 .

$\phi\left(\frac{x_1 - M_1}{\sigma_1}\right)$	x_1
0.00023	$M_1 - 3.5\sigma_1$
0.0013	$M_1 - 3\sigma_1$
0.0228	$M_1 - 2\sigma_1$
0.1587	$M_1 - \sigma_1$
0.5000	M_1
0.8413	$M_1 + \sigma_1$
0.9772	$M_1 + 2\sigma_1$
0.9987	$M_1 + 3\sigma_1$
0.99977	$M_1 + 3.5\sigma_1$

In Fig. 2, $P(x_1; M_1, \sigma_1)$ is plotted against x_1 for some specific mean values M_1 and standard deviations σ_1 . For a given x_1 , M_1 , and σ_1 , $\phi[(x_1 - M_1)/\sigma_1]$ can be obtained from the *Biometrika table for statisticians* (Ref. 8).

Another consideration governing the specific growth rate is the existence of an endogenous metabolism that

continues even in the absence of growth. It is considered in the present study as a constant B_1 . Hence, the specific growth rate of the three organisms (x_1 , x_2 , and Y) can be expressed as

$$\mu_1 = \mu_{m1} \frac{s}{k_1 + s} P(x_1; M_1, \sigma_1) - B_1 \quad (15)$$

$$\mu_2 = \mu_{m2} \frac{s}{k_2 + s} P(x_2; M_2, \sigma_2) - B_2 \quad (16)$$

$$\mu_y = \mu_{my} \frac{x_1}{k_y + x_1} P(y; M_y, \sigma_y) - B_y \quad (17)$$

where μ_{m2} and μ_{my} are the maximum values of μ for x_2 and y , respectively.

The differential equations of the three-component system can be obtained from Eqs. (7-10) by setting $x_2 = 0$. This yields

$$\frac{dx_1}{dt} = x_1(\mu_1 - D) - \frac{\mu_y y}{c_y} \quad (18)$$

$$\frac{dy}{dt} = y(\mu_y - D) \quad (19)$$

$$\frac{ds}{dt} = D(s_r - s) - \frac{\mu_1 x_1}{c_1} \quad (20)$$

$$\mu_1 = \mu_{m1} \frac{s}{k_1 + s} P(x_1; M_1, \sigma_1) - B_1 \quad (21)$$

$$\mu_y = \mu_{my} \frac{x_1}{k_y + x_1} P(y; M_y, \sigma_y) - B_y \quad (22)$$

The dynamic response of these two systems is examined in this study.

IV. Numerical Analysis

A. Numerical Solution of Dynamic Response

Equations (7-10) are a set of first-order nonlinear differential equations belonging to the initial value problem. The numerical method of solution for the initial value problem is to convert a set of differential equations into a set of difference equations (schemes) and then to perform step-by-step integration.

There are several techniques available for the approximate solution of such a set of differential equations by

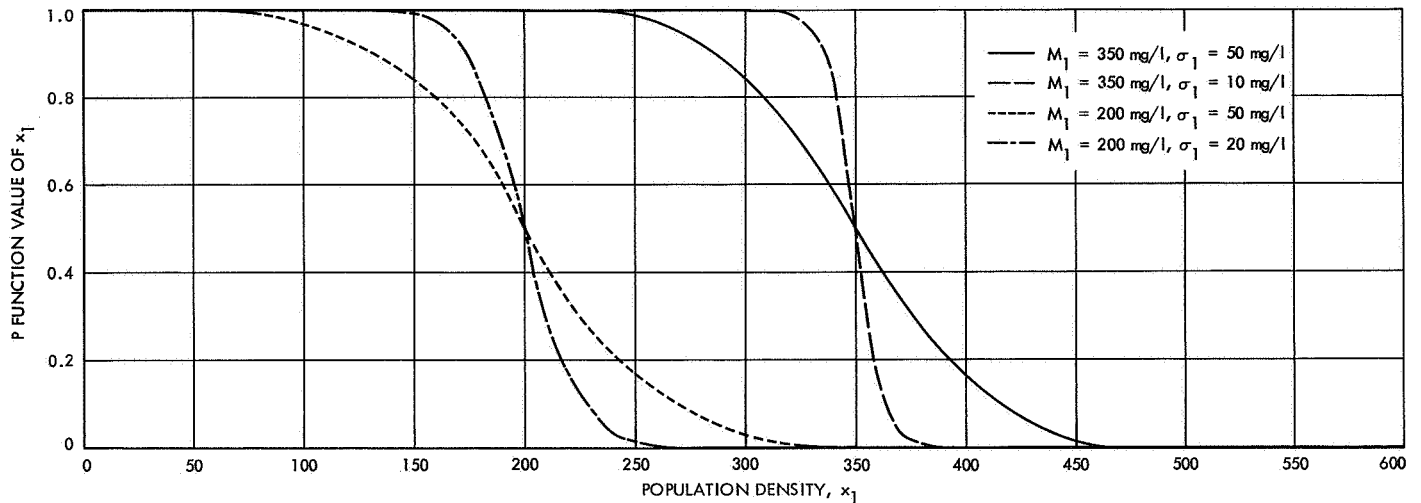


Fig. 2. Illustration of the effect of M and σ on the P function

numerical methods. In this study, the technique of the fourth-order Adams–Moulton predictor–corrector method is employed with the classical fourth-order Runge–Katta method used for starting. Further discussions of numerical methods can be found in Refs. 9 and 10.

The difference scheme is coded into a program for the 7094 computer.

B. Steady-State Solution

The steady-state solution is obtained by setting the derivatives of all variables to zero.

$$\frac{dx_1}{dt} = 0, \frac{ds}{dt} = 0, \frac{dx_2}{dt} = 0, \frac{dy}{dt} = 0$$

Hence, it follows from Eqs. (7–10) and (15–17) that

$$\bar{x}_1(\bar{\mu}_1 - D) - \frac{\bar{\mu}_y \bar{y}}{c_y} = 0 \quad (23)$$

$$D(s_r - \bar{s}) - \frac{\bar{\mu}_1 \bar{x}_1}{c_1} - \frac{\bar{\mu}_2 \bar{x}_2}{c_2} = 0 \quad (24)$$

$$\bar{x}_2(\bar{\mu}_2 - D) = 0 \quad (25)$$

$$\bar{y}(\bar{\mu}_y - D) = 0 \quad (26)$$

where the expression with a bar represents the value at the steady state, and

$$\bar{\mu}_1 = \mu_{m1} \frac{\bar{s}}{k_1 + \bar{s}} P(\bar{x}_1; M_1, \sigma_1) - B_1 \quad (27)$$

$$\bar{\mu}_2 = \mu_{m2} \frac{\bar{s}}{k_2 + \bar{s}} P(\bar{x}_2; M_2, \sigma_2) - B_2 \quad (28)$$

$$\bar{\mu}_y = \mu_{my} \frac{\bar{x}_1}{k_y + \bar{x}_1} P(\bar{y}; M_y, \sigma_y) - B_y \quad (29)$$

The steady state $(\bar{x}_1, \bar{x}_2, \bar{y}, \bar{s})$ can be obtained by substituting Eqs. (27–29) into Eqs. (23–26). It can be seen that several possible steady states exist. For example, one of the steady states is $\bar{x}_2 = 0, \bar{x}_1 > 0, \bar{s} > 0, \bar{y} > 0$; another steady state is $\bar{x}_1 = 0, \bar{y} = 0, \bar{x}_2 > 0, \bar{s} > 0$, etc. However, we are most interested in the steady state at which all the variables coexist.

It is unlikely that the steady state of the coexistence of four variables can occur at high values of x_1, x_2 , and y . This follows from our setting $M_1 = M_2 = M_y = 350 \text{ mg/l}$ and $\sigma_1 = \sigma_2 = \sigma_y = 50 \text{ mg/l}$ in this study. It can be seen from Fig. 2 that $P(\bar{x}_1; M_1, \sigma_1) \simeq 1$ for $\bar{x}_1 < 200 \text{ mg/l}$. Therefore, we assume $P(\bar{x}_1; M_1, \sigma_1) = 1, P(\bar{x}_2; M_2, \sigma_2) = 1$ and $P(\bar{y}; M_y, \sigma_y) = 1$, and solve for $\bar{x}_1, \bar{x}_2, \bar{y}$ and \bar{s} as follows:

$$\bar{x}_1 = \frac{k_y(D + B_y)}{\mu_{my} - (D + B_y)} \quad (30)$$

$$\bar{s} = \frac{k_2(D + B_2)}{\mu_{m2} - (D + B_2)} \quad (31)$$

$$\bar{y} = \frac{c_y \bar{x}_1}{\bar{\mu}_y} (\bar{\mu}_1 - D) \quad (32)$$

$$\bar{x}_2 = \frac{c_2}{\bar{\mu}_2} \left[D(s_r - \bar{s}) - \frac{\bar{x}_1 \bar{\mu}_1}{c_1} \right] \quad (33)$$

In case any of \bar{x}_1 , \bar{x}_2 , and \bar{y} obtained from Eqs. (30–33) is greater than 200 mg/l, the steady state (\bar{x}_1 , \bar{x}_2 , \bar{y} , \bar{s}) should be solved numerically directly from Eqs. (23–29). Similarly, the coexistence steady state of the three-variable system is

$$\bar{x}_1 = \frac{k_y (D + B_y)}{\mu_{my} - (D + B_y)} \quad (34)$$

$$\bar{s} = q + (q^2 + g)^{1/2} \quad (35)$$

$$\bar{y} = \frac{c_y \bar{x}_1}{\bar{\mu}_y} (\bar{\mu}_1 - D) \quad (36)$$

where

$$q = \frac{1}{2} \left(s_r - k_1 - \frac{\mu_{m1}}{Dc_1} \bar{x}_1 + \frac{B_1}{Dc_1} \bar{x}_1 \right) \quad (37)$$

$$g = s_r k_1 + \frac{B_1}{Dc_1} \bar{x}_1 k_1 \quad (38)$$

C. Stability Criterion of the Steady State

The fact that a steady state is possible does not automatically imply that the system will ever reach this state (see, for example, Ref. 11). It is extremely important to know whether the steady state of interest is stable or not, so that we may know if the system will reach that steady state. From the stability analysis, one can predict under what circumstances or with what parameter values (such as dilution rate, resource concentration, etc.) a steady state of interest is stable. Conditions for the stability of any possible steady state are given explicitly as follows:

Let

$$x_1 = \bar{x}_1 + \Delta x_1 \quad (39a)$$

$$s = \bar{s} + \Delta s \quad (39b)$$

$$x_2 = \bar{x}_2 + \Delta x_2 \quad (39c)$$

$$y = \bar{y} + \Delta y \quad (39d)$$

with $\Delta x_1 \ll \bar{x}_1$, $\Delta x_2 \ll \bar{x}_2$, $\Delta s \ll \bar{s}$, and $\Delta y \ll \bar{y}$.

After expanding Eqs. (7–10) into a Taylor's series about a steady state (\bar{x}_1 , \bar{x}_2 , \bar{y} , \bar{s}) and retaining only the first-order terms of Δx_1 , Δx_2 , Δs , and Δy , one can obtain the following results by using Eqs. (39a–39d).

$$\frac{d\Delta x_1}{dt} = a_{11} \Delta x_1 + a_{12} \Delta s + a_{13} \Delta x_2 + a_{14} \Delta y \quad (40a)$$

$$\frac{d\Delta s}{dt} = a_{21} \Delta x_1 + a_{22} \Delta s + a_{23} \Delta x_2 + a_{24} \Delta y \quad (40b)$$

$$\frac{d\Delta x_2}{dt} = a_{31} \Delta x_1 + a_{32} \Delta s + a_{33} \Delta x_2 + a_{34} \Delta y \quad (40c)$$

$$\frac{d\Delta y}{dt} = a_{41} \Delta x_1 + a_{42} \Delta s + a_{43} \Delta x_2 + a_{44} \Delta y \quad (40d)$$

where

$$a_{11} = \bar{\mu}_1 - D + \bar{x}_1 \frac{\partial \bar{\mu}_1}{\partial x_1} - \frac{1}{c_y} \bar{y} \frac{\partial \bar{\mu}_y}{\partial x_1} \quad (41a)$$

$$a_{12} = \bar{x}_1 \frac{\partial \bar{\mu}_1}{\partial s} \quad (41b)$$

$$a_{13} = 0 \quad (41c)$$

$$a_{14} = -\frac{1}{c_y} \left(\bar{\mu}_y + \bar{y} \frac{\partial \bar{\mu}_y}{\partial y} \right) \quad (41d)$$

$$a_{21} = -\frac{1}{c_1} \left(\bar{\mu}_1 + \bar{x}_1 \frac{\partial \bar{\mu}_1}{\partial x_1} \right) \quad (41e)$$

$$a_{22} = -\left(D + \frac{1}{c_1} \bar{x}_1 \frac{\partial \bar{\mu}_1}{\partial s} + \frac{1}{c_2} \bar{x}_2 \frac{\partial \bar{\mu}_2}{\partial s} \right) \quad (41f)$$

$$a_{23} = -\frac{1}{c_2} \left(\bar{\mu}_2 + \bar{x}_2 \frac{\partial \bar{\mu}_2}{\partial x_2} \right) \quad (41g)$$

$$a_{24} = 0 \quad (41h)$$

$$a_{31} = 0 \quad (41i)$$

$$a_{32} = \bar{x}_2 \frac{\partial \bar{\mu}_2}{\partial s} \quad (41j)$$

$$a_{33} = \bar{x}_2 \frac{\partial \bar{\mu}_2}{\partial x_2} + \bar{\mu}_2 - D \quad (41k)$$

$$a_{34} = 0 \quad (41l)$$

$$a_{41} = \bar{y} \frac{\partial \bar{\mu}_y}{\partial x_1} \quad (41m)$$

$$a_{42} = 0 \quad (41n)$$

$$a_{43} = 0 \quad (41o)$$

$$a_{44} = \bar{y} \frac{\partial \bar{\mu}_y}{\partial y} + \bar{\mu}_y - D \quad (41p)$$

with $\bar{\mu}_1, \bar{\mu}_2, \bar{\mu}_y$ being given in Eqs. (27-29) and $\partial \bar{\mu}_1 / \partial x_1$ representing the partial derivatives of μ_1 with respect to x_1 , evaluated at the steady state.

Similar definitions apply for $\partial \bar{\mu}_1 / \partial s, \partial \bar{\mu}_y / \partial x_1, \partial \bar{\mu}_2 / \partial s$, etc. These quantities can be obtained as follows:

$$\begin{aligned} \frac{\partial \bar{\mu}_1}{\partial x_1} = & -\mu_{m1} \frac{\bar{s}}{k_1 + \bar{s}} \frac{1}{(2\pi)^{1/2} \sigma_1} \\ & \times \exp \left[-\frac{1}{2} \left(\frac{\bar{x}_1 - M_1}{\sigma_1} \right)^2 \right] \end{aligned} \quad (42a)$$

$$\frac{\partial \bar{\mu}_1}{\partial s} = \mu_{m1} \frac{k_1}{(k_1 + \bar{s})^2} P(\bar{x}_1; M_1, \sigma_1) \quad (42b)$$

$$\begin{aligned} \frac{\partial \bar{\mu}_2}{\partial x_2} = & -\mu_{m2} \frac{\bar{s}}{k_2 + \bar{s}} \frac{1}{(2\pi)^{1/2} \sigma_2} \\ & \times \exp \left[-\frac{1}{2} \left(\frac{\bar{x}_2 - M_2}{\sigma_2} \right)^2 \right] \end{aligned} \quad (42c)$$

$$\frac{\partial \bar{\mu}_2}{\partial s} = \mu_{m2} \frac{k_2}{(k_2 + \bar{s})^2} P(\bar{x}_2; M_2, \sigma_2) \quad (42d)$$

$$\begin{aligned} \frac{\partial \bar{\mu}_y}{\partial y} = & -\mu_{my} \frac{\bar{x}_1}{k_y + \bar{x}_1} \frac{1}{(2\pi)^{1/2} \sigma_y} \\ & \times \exp \left[-\frac{1}{2} \left(\frac{\bar{y} - M_y}{\sigma_y} \right)^2 \right] \end{aligned} \quad (42e)$$

$$\frac{\partial \bar{\mu}_y}{\partial x_1} = \mu_{my} \frac{k_y}{(k_y + \bar{x}_1)^2} P(\bar{y}; M_y, \sigma_y) \quad (42f)$$

It can be shown that the steady-state solution $(\bar{x}_1, \bar{x}_2, \bar{s}, \bar{y})$ is stable if and only if the real parts of all the eigenvalues of matrix **A** are negative (Refs. 12 and 13), where

$$\mathbf{A} = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{bmatrix} \quad (43)$$

In other words, the real parts of all the roots of the characteristic equation, say $\lambda_1, \lambda_2, \lambda_3$ and λ_4 , are negative where the characteristic equation is

$$\begin{vmatrix} a_{11} - \lambda & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} - \lambda & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} - \lambda & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} - \lambda \end{vmatrix} = 0 \quad (44)$$

Equation (44) can be solved numerically, for a given steady state $(\bar{x}_1, \bar{x}_2, \bar{y}, \bar{s})$, to obtain the four roots of λ , whereas a_{ij} ($i = 1, 2, 3, 4; j = 1, 2, 3, 4$) are given explicitly in Eqs. (41), (42), (27), (28), and (29).

It should be mentioned that if any of the roots are complex but all with negative real parts, the steady state is stable but with damped oscillation.

The stability criterion can also be obtained without solving the eigenvalues. Equation (44) can be written as a fourth-order polynomial in λ :

$$a_0 \lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0 \quad (45)$$

for $a_0 > 0$. According to the Routh-Hurwitz criterion, all the roots of λ have negative real parts if and only if the following determinantal inequalities hold:

$$\begin{aligned} & |a_1| > 0 \\ & \begin{vmatrix} a_1 & a_3 \\ a_0 & a_2 \end{vmatrix} > 0 \\ & \begin{vmatrix} a_1 & a_3 & 0 \\ a_0 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix} > 0 \\ & \begin{vmatrix} a_1 & a_3 & 0 & 0 \\ a_0 & a_2 & a_4 & 0 \\ 0 & a_1 & a_3 & 0 \\ 0 & a_0 & a_2 & a_4 \end{vmatrix} > 0 \end{aligned} \quad (46)$$

The stability analysis in this section is quite general. It can be generalized to the system with any number of resources, preys, and predators.

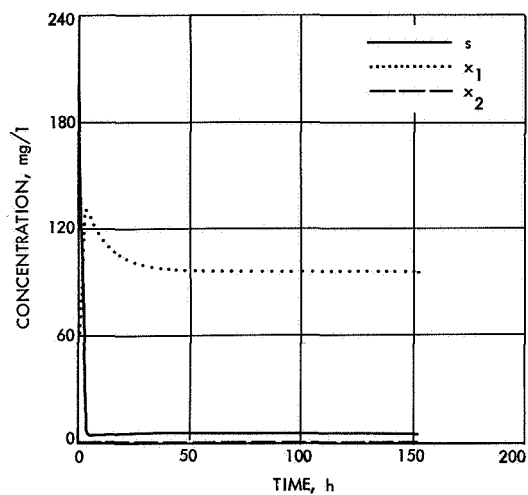


Fig. 3. Equilibrium level of species X_1 and its limiting resource S when there is no competition for the resource and no predation

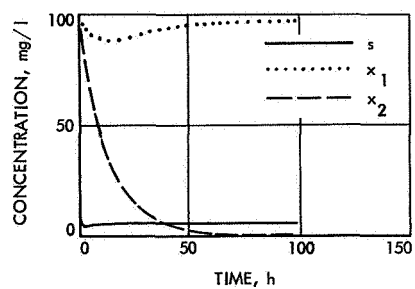


Fig. 4. Unsuccessful competition of species X_2 for resource S in the absence of predation

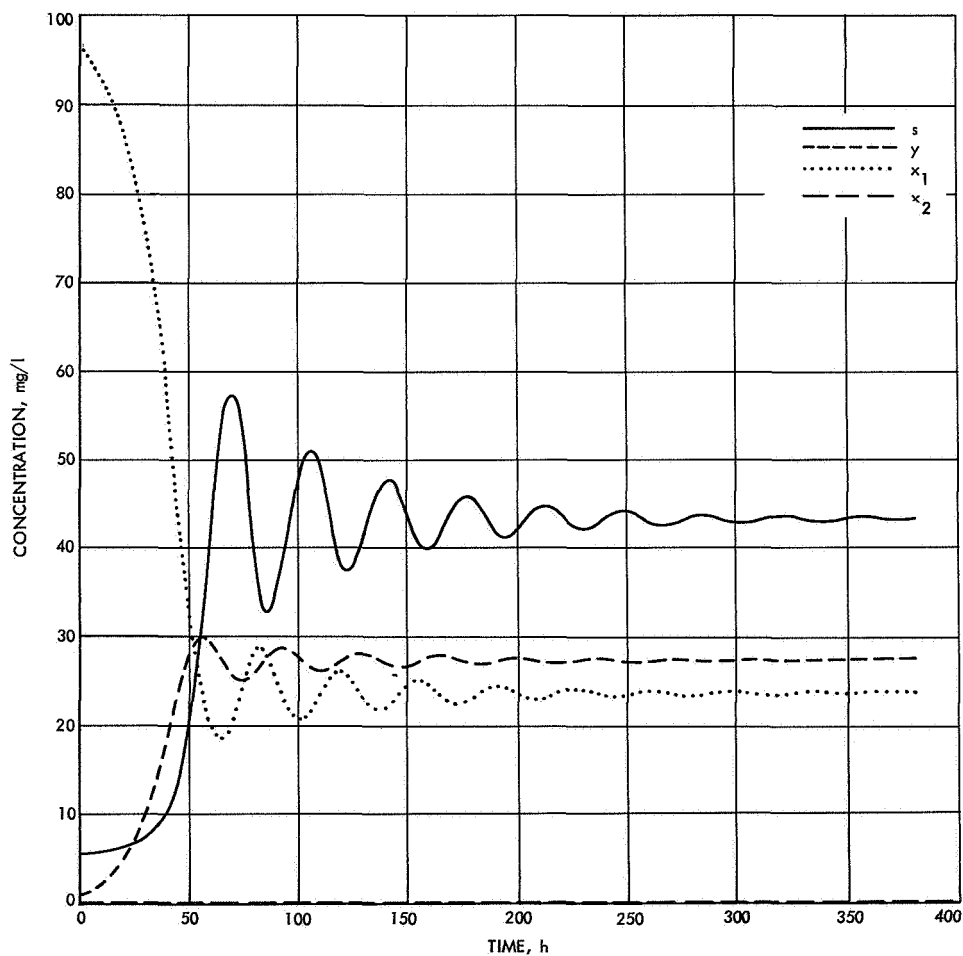


Fig. 5. Increased level of resource S when predator Y preys upon X_1 (three-variable system)

V. Numerical Results

The numerical results for the following set of values are plotted throughout this section, unless otherwise stated.

$$D = 0.1 \text{ h}^{-1}$$

$$s_r = 200 \text{ mg/l}$$

$$B_1 = B_2 = B_y = 0.01 \text{ h}^{-1}$$

$$\mu_{m1} = 0.5 \text{ h}^{-1}, \mu_{m2} = 0.25 \text{ h}^{-1}, \mu_{my} = 0.25 \text{ h}^{-1}$$

$$k_1 = 20 \text{ mg/l}, k_2 = 35 \text{ mg/l}, k_y = 30 \text{ mg/l}$$

$$c_1 = c_2 = c_y = 0.5$$

$$M_1 = M_2 = M_y = 350 \text{ mg/l}$$

$$\sigma_1 = \sigma_2 = \sigma_y = 50 \text{ mg/l}$$

When x_2 and y are set at zero for the initial conditions, the standard chemostat equilibrium for \bar{x}_1 and \bar{s} is obtained (Fig. 3). When X_2 is added at the concentration of \bar{x}_1 , X_1 begins to decrease as it is deprived of some nutrients used by X_2 ; but it soon returns to its original level, while X_2 is washed out of the system in agreement with the expectation of competitive exclusion (Fig. 4). When Y is added at $1/100$ the concentration of \bar{x}_1 , the three-variable system begins to oscillate with a damped period and finally arrives at a coexistence steady state (Fig. 5). It is found from the stability analysis that this

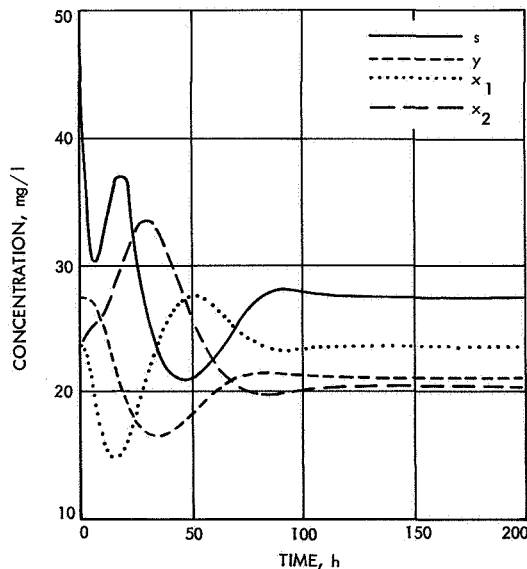


Fig. 6. Coexistence steady state of X_2 and X_1 when X_1 is preyed upon by Y (four-variable system)

is a stable steady state. Note that s never falls back to its original level. Now, with addition of X_2 , again at the concentration of \bar{x}_1 , the four-variable system rapidly stabilizes at a coexistence equilibrium. Again, this is a stable steady state (Fig. 6).

A. Effect of B_1 , B_2 , and B_y

When values of B_1 , B_2 , and B_y are decreased to 0.001 h^{-1} , the three-variable system begins to oscillate with a regular undamped period of 40 h (Fig. 7); it is found from the stability analysis that the system has no stable steady state. If B_1 , B_2 , and B_y are zero, the system oscillates at the same period but with higher amplitudes. Again, the system has no stable steady state (Fig. 8). However, with these changes of B_1 , B_2 , and B_y , the four-variable system still converges to the coexistence steady state, which is stable, according to stability analysis.

B. Change of Dilution Rate

If the dilution rate D is reduced to 0.07 h^{-1} , the three-variable system has no steady state and oscillates with a period of 40 h (Fig. 9), but the four-variable system is stable at the coexistence steady state, which is achieved after several damped oscillations (Fig. 10). When D is increased to 0.15 h^{-1} , the three-variable system becomes

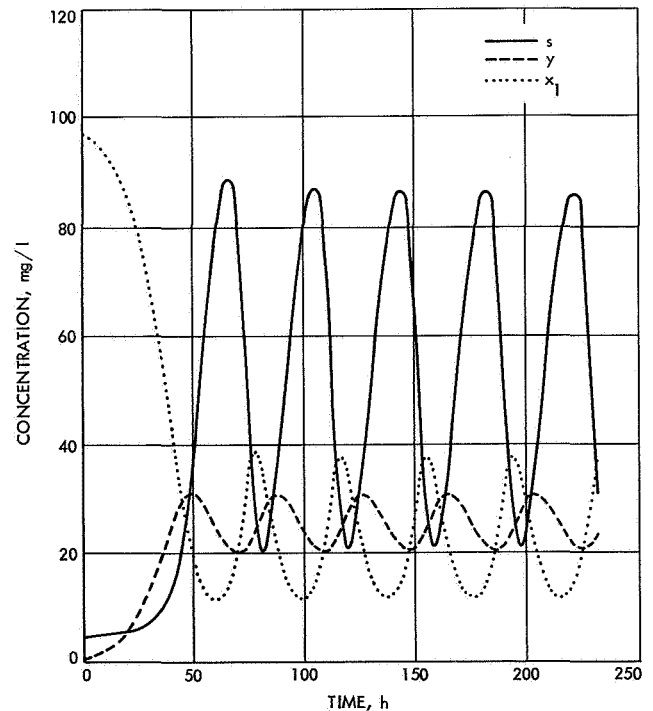


Fig. 7. Effect of level of endogeneous metabolism B on three-variable system when $B = 0.001$

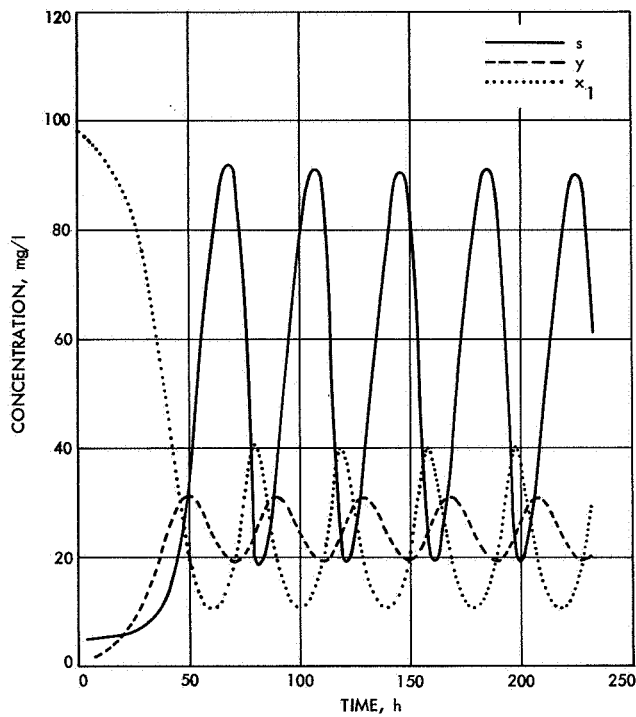


Fig. 8. Effect of level of endogenous metabolism B on three-variable system when $B=0.0$

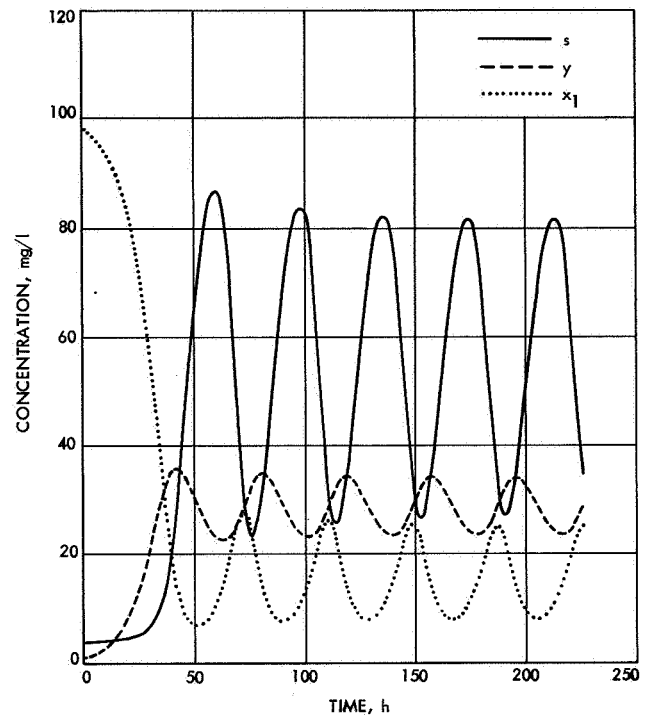


Fig. 9. Effect of dilution rate D on three-variable system when $D=0.07$

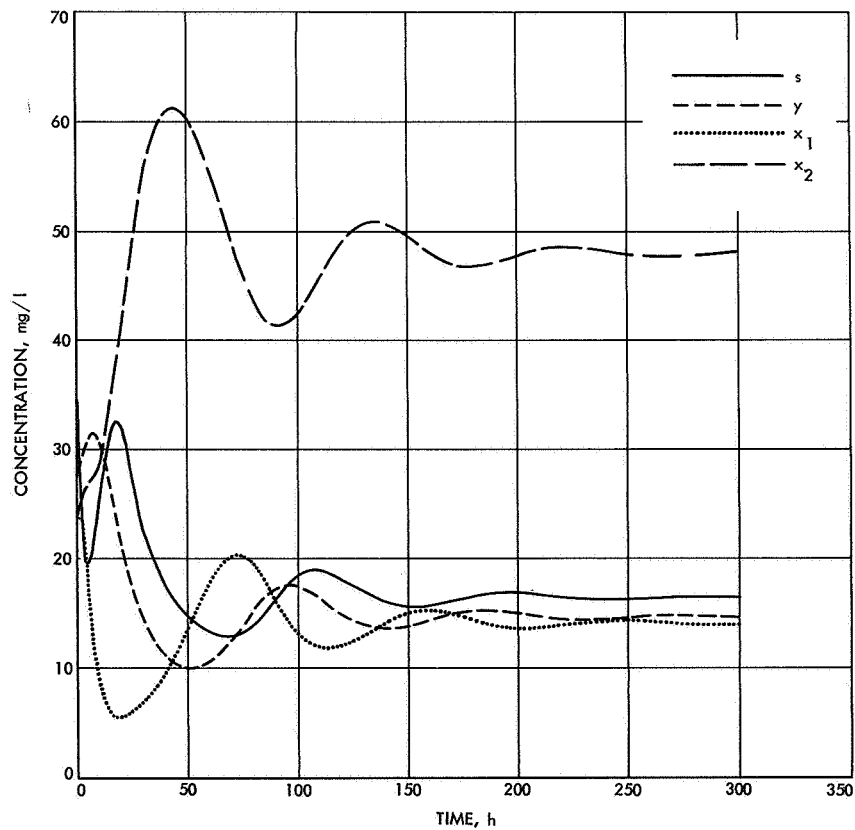


Fig. 10. Effect of dilution rate D on four-variable system at $D=0.07$

stable at the coexistence steady state and converges quickly (Fig. 11), while the four-variable system has no stable coexistence steady state. In this case X_2 cannot persist in the system. Hence, as X_2 is washed out, the system converges (Fig. 12) to the same steady state as the three-variable system (Fig. 11).

C. Changed Input Substrate Concentration

If s_r is decreased to 150 mg/l, the three-variable system converges quickly to the coexistence steady state

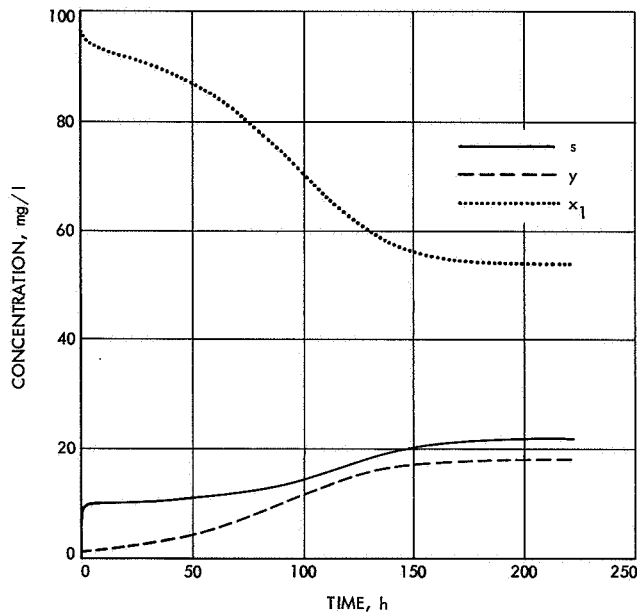


Fig. 11. Effect of dilution rate D on three-variable system when $D = 0.15$

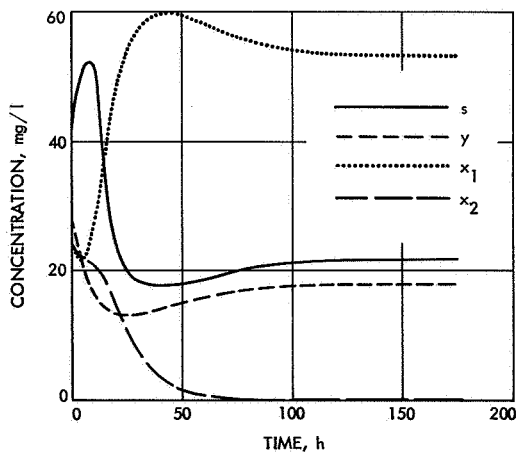


Fig. 12. Effect of dilution rate D on four-variable system. Note that X_2 is unsuccessful at $D = 0.15 \text{ h}^{-1}$, reverting to three-variable system

(Fig. 13), while the four-variable system becomes unstable at the coexistence steady state. Again X_2 is lost from the system and the system converges to the same steady state as the corresponding three-variable system (Fig. 14). When s_r is increased to 250 mg/l, the three-variable system has no stable steady state and oscillates at a regular period of 40 h (Fig. 15), while the four-variable system is stable at the coexistence steady state (Fig. 16).

To summarize, with this particular set of parameters, it is found that the four-variable system is always stable at one of the possible steady states, while the three-variable system may stabilize, but more frequently it exhibits considerable oscillations (none of the possible steady states is stable).

VI. Discussion

Based upon our assumptions and under the conditions tested, we have demonstrated that there is a theoretical expectation that (1) the level of resource concentration rises when the consumer population is reduced by predation, and (2) an additional consumer can coexist with the original consumer utilizing the resources released by predation. These two observations are in full agreement with the suggestion by Paine. Moreover, we have seen that the presence of the second consumer stabilizes a predator-prey association which otherwise might oscillate.

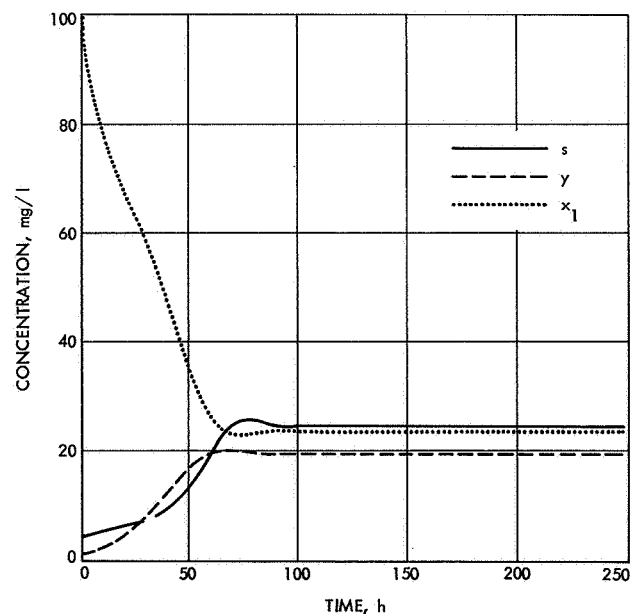


Fig. 13. Effect of input resource concentration s_r on three-variable system ($s_r = 150 \text{ mg/l}$)

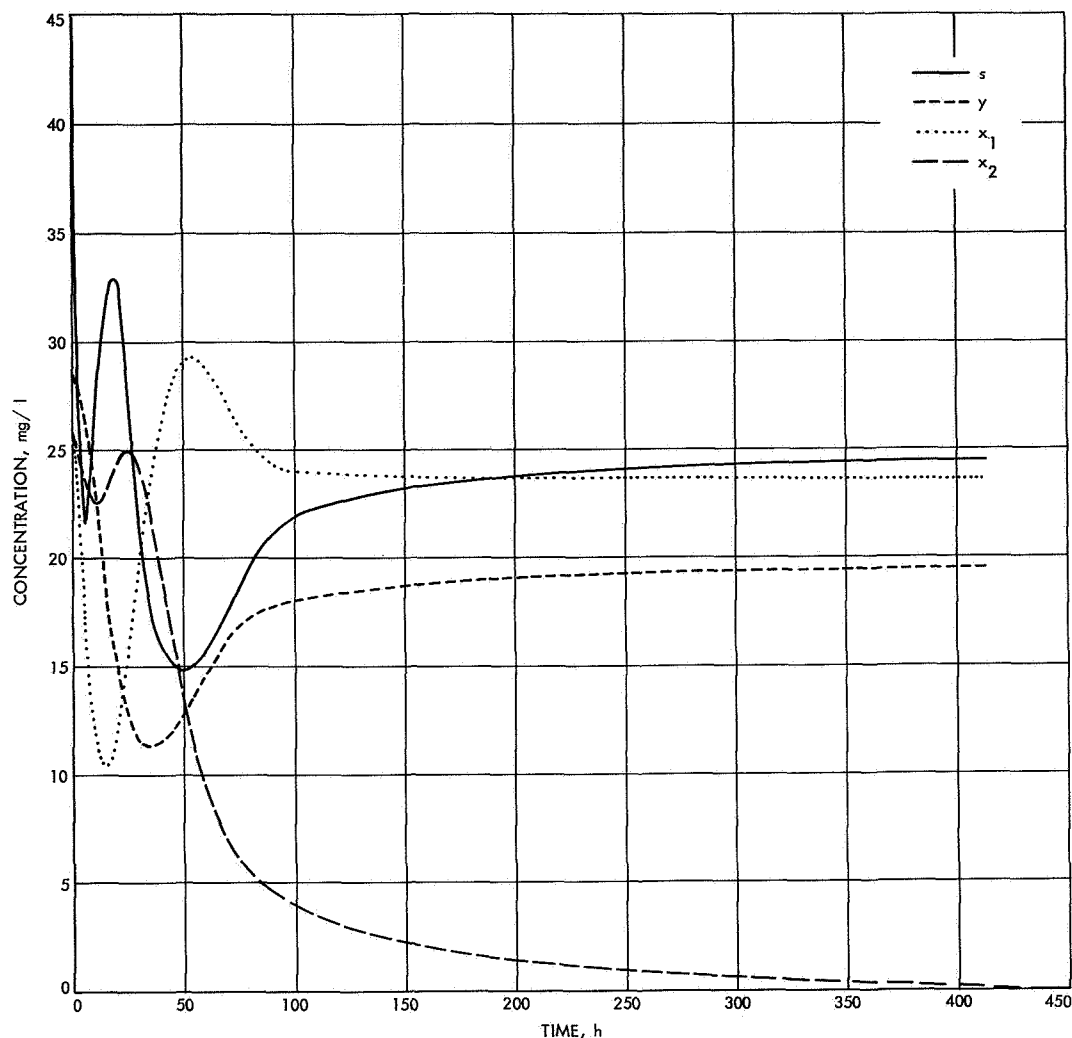


Fig. 14. Effect of input resource concentration s_r on four-variable system (note that X_2 is unsuccessful at $s_r = 150 \text{ mg/l}$, reverting to three-variable system)

To what degree do these conclusions depend upon the foregoing conditions and assumptions? Before examining the specific assumptions, we must consider more generally the conditions which will lead to coexistence. Regardless of the mechanism and interactions which may be involved, the persistence of a species in an environment depends fundamentally upon whether the replacement of the population by reproduction, growth, and immigration is equal to loss from all causes (predation, old age, disease, emigration, etc.).*

A corollary of this observation is that a newly introduced species can become a permanent member of the community only if its intrinsic growth exceeds its loss. This

*Temporarily, population gain may exceed the losses or vice versa; but in time, gains and losses must be equal.

corollary does not predict how numerous the population will be at equilibrium (or whether a steady state will be reached—as opposed to oscillation), since rate of gain and rate of loss may be environmentally controlled, density dependent, or resource limited. However, failure of the introduced species can be predicted if: (1) there is no inoculum level at which growth can exceed losses, and (2) there is no interaction between the introduced species and the components of the environment (resources, competitors, predators, etc.) that can alter the environment such that the first proviso applies. Thus, in the chemostat, if X_1 maintains s at a level where $\mu_2 < D$, then Eq. (8) has a negative value and X_2 will disappear. Any circumstance which alters the value of μ or D for either of the two competitors will alter the prospect for coexistence.

Further discussion will concern which circumstances can lead to coexistence, as well as limitations in the model.

A. The Chemostat Model

The most restrictive assumption of this analysis of predator-prey interaction lies in taking the chemostat as

a model. Two important constraints result: First, primary resource in the chemostat model is renewed at a rate independent of the level of resource in the environment. This might be the case of litter accumulating from falling leaves, but if the resource were taken to be foliage on the plant or aquatic algae, its regeneration should reflect a concentration dependence. For example, the differential expression, Eq. (10), might be replaced by:

$$\frac{ds}{dt} = \mu_s s - Ds - \frac{\mu_1 x_1}{c_1} - \frac{\mu_2 x_2}{c_2} \quad (47)$$

Second, the rate of removal of x_1 , x_2 , s , and y from all causes but consumption at the next higher trophic level is built into the value of the dilution rate D . In natural environments the rate of loss to other predators, such as disease, emigration, etc., would not be the same for s , x_1 , x_2 , and y . This limitation can be removed simply by specifying a unique D value, D_s , D_1 , D_2 , D_y , for s , x_1 , x_2 , and y .

It can be expected that the incorporation of these more general assumptions might alter the behavior of the model in several ways. Making the regenerating of s a function of its own concentration might: (1) introduce oscillations in the X_1 , S association, (2) partially or completely dampen the X_1 , S , Y complex, and (3) alter period and amplitude of the X_1 , X_2 , S , Y complex.

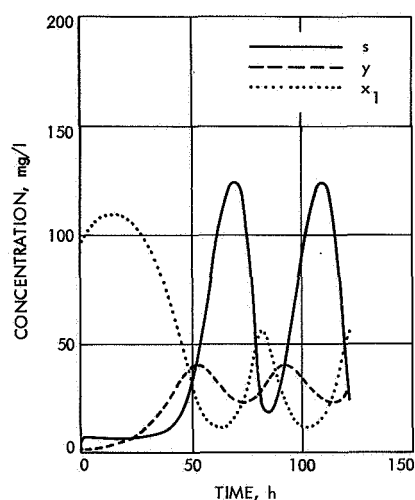


Fig. 15. Effect of input resource concentration s_r on three-variable system ($s_r = 250$ mg/l)

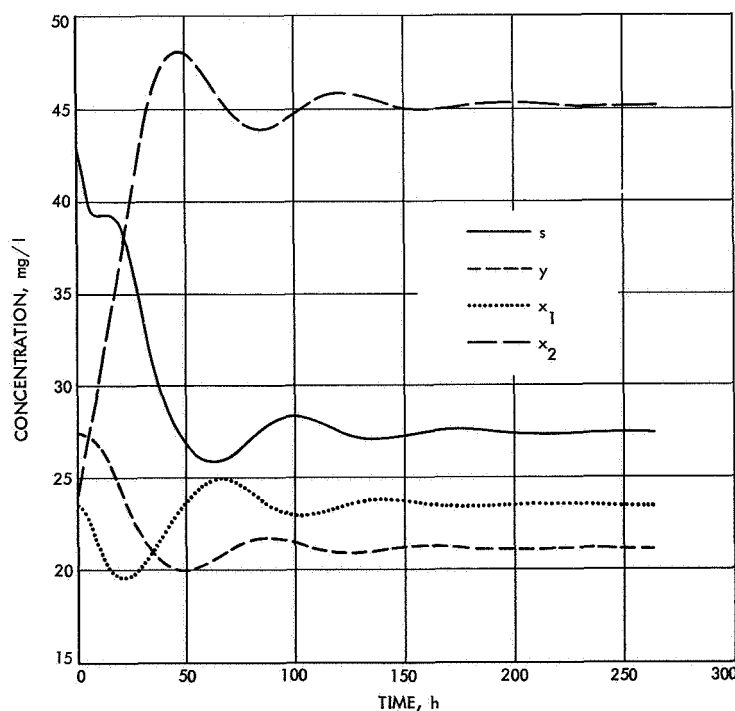


Fig. 16. Effect of input resource concentration s_r on four-variable system ($s_r = 250$ mg/l)

Applying specific values of D to each organism should lead to far more complex interactions and thus a larger variety of relations resulting in steady states, but should not alter the present observations that an additional consumer *can* coexist on resources released by predation. Of course, these expectations need to be tested.

B. Formulation of the P Function

The $P(x_1; M_1, \sigma_1)$ function has been defined generally as having the property that its values be near zero when populations are high and near one when populations are low, and defined specifically by Eq. (13). From an examination of how $P(x_1; M_1, \sigma_1)$ affects the model interactions, the probable effect of functions other than the one we have used can be deduced.

From the view of the introduced consumer X_2 , the most important effect of $P(x_1; M_1, \sigma_1)$ is in limiting the rate at which S is consumed by X_1 . As previously noted, a steady state is reached when μ_1 equals D . If μ_1 is not to be depressed as $P(x_1; M_1, \sigma_1)$ is lowered (increased population inhibition), the equality in Eq. (15) must be maintained by an increase in S . The increased level of s will result in a higher μ_2 . If $\mu_2 > D$ as a result of higher s , then X_2 will grow in the system. In general, under conditions of crowding that lead to $\mu_2 > \mu_1$, there may be coexistence of X_1 and X_2 .

For a given D , and not considering the effect of $P(x_1; M_1, \sigma_1)$, the value of x_1 will depend upon the relative magnitude of k_1 and k_2 .

To determine the effect of varying $P(x_1; M_1, \sigma_1)$, we may consider two functions of $P(x_1; M_1, \sigma_1)$, where both have some low value [e.g., $P(x_1; M_1, \sigma_1) = 0.01$] at the same level of crowding of X_1 . That is, the growth of X_1 is nearly completely inhibited at the same population density with either function. However, the first passes from near 1 [e.g., $P(x_1; M_1, \sigma_1) = 0.99$] to 0.01 over a narrow range of values of x_1 , while for the second, the transition of $P(x_1; M_1, \sigma_1)$ from 0.99 to 0.01 begins at a lower concentration of x_1 and takes place over a broader range of concentrations.

In general, the lower the value of x_1 at which $P(x_1; M_1, \sigma_1)$ departs significantly from 1 the more likely it is that, for any value of s_r , coexistence will result. Furthermore, the higher the value of s_r , regardless of the nature of $P(x_1; M_1, \sigma_1)$, the more likely that $P(x_1; M_1, \sigma_1)$ departs from 1 and that X_1 and X_2 coexist. As $c_1 s_r$ approaches the limiting population of X_1 , then $P(x_1; M_1, \sigma_1)$ approaches 0; hence, the probability of coexistence increases.

In conclusion, the incorporation of $P(x_1; M_1, \sigma_1)$ determines that there will be some level of s_r where $\mu_2 > D$, that is, where x_2 can coexist with x_1 , while the specific nature of $P(x_1; M_1, \sigma_1)$ determines the range of s_r values over which coexistence can occur. Except where a particular natural association is being modeled, our conclusions are unaffected as long as $P(x_1; M_1, \sigma_1)$ is a function that satisfies the transition from one to zero.

C. The Formulation of Growth Rate

As with $P(x_1; M_1, \sigma_1)$, the general characteristics of μ are more important than the particular formulation. If μ were a constant at all values of resource, interactions between consumers would be governed solely by $P(x_1; M_1, \sigma_1)$; specifically, coexistence would only become possible at relatively high population densities. On the other hand, different μ functions, which displayed the transition from zero in the absence of resource to some maximum at all large concentrations of resource, would all lead to the type of predator-consumer-resource interactions we have studied. As with $P(x_1; M_1, \sigma_1)$, the particular function for μ will determine the particular concentrations with which continuous oscillation, steady-state coexistence, or exclusion will occur.

D. Deterministic vs Stochastic Solutions

The stated solution for the predator-consumer-resource interaction is, of course, oversimplified. Other predators, alternate prey, other consumers, behavioral modifications (mimicry, hiding, diurnal rhythms, defense postures), and environmental fluctuations would influence the outcome of competition or predation in almost any natural community.

To introduce any additional biological interactions would be to establish a new problem with a new set of descriptive equations. However, random fluctuations of temperature, available water, oxygen, and other environmental parameters could be expected to alter the value of different constants within the context of the present formulation. Such fluctuations might be amplified and, in certain cases, they might set up resonances which would upset a system thought to be stable from deterministic analysis (Ref. 14). Thus, the added realism of a stochastic model and the expectation of significant interactions from random perturbations are strong arguments for reanalyzing the model with stochastic processes.

Our conclusions conflict with those of Spight, who argued that the preyed-upon population can alter its rate of resource utilization in such a way that the level

of resource remains unchanged even in the presence of a predator. He concluded that "... additional factors must be invoked to explain the existence of the resources which support . . . additional species," since ". . . prey populations apparently make the required response to different schemes and intensities of predation" (Ref. 2). To what extent does our formulation of the growth model conform to his expectation that organisms "... make the required response . . ." to predation, such that their utilization of resources is constant regardless of population density?

If s is to be constant, Eq. (20) must be valued at zero for all values of x_1 . This requires that $\mu_1 x_1 / c_1$ has a constant value since D and s_r are constant. Since x_1 is clearly a variable, the values of c_1 or μ_1 (or both) would have to be compensating variable functions of x_1 .

The yield factor c_1 is probably around 0.5 at its maximum for microorganisms, and lower for more complex forms. If c_1 were to vary with population density to satisfy $\mu_1 x_1 / c_1 = \text{constant}$, it would have to have its maximum value at the maximum population, and decrease with lower populations. Thus, when x_1 is at one hundredth of

its maximum population, then $c_1 = 0.005$. Such a low conversion yield factor is not observed. In fact, c_1 is experimentally observed to be nearly constant over wide population levels, and the variation which is observed is in the opposite direction; i.e., at higher population, the yield is lower. (See, for example, Ref. 15.)

Thus, only if μ_1 varies inversely with x_1 can we satisfy the condition that $\mu_1 x_1 / c_1$ is invariant with x_1 . Indeed, at high population densities, such a relation (or one similar) must apply, since it is demonstrable experimentally that growth rate approaches zero as an upper population limit is approached. However, the implication of the inverse function for low population (that μ_1 can increase without limit) is biologically unacceptable. Rather, the observation is that at any low population a maximum growth rate μ_{m1} is approached providing only that all resources are made available in excess. Thus, we have chosen to represent growth as a function of nutrient concentration and population density, so that the growth rate is sensitive to s at low nutrient levels and sensitive to x_1 at high population levels. The assumptions which would support Spight's conclusions are apparently not biologically valid.

Nomenclature

B	endogenous metabolism which continues in the absence of growth	V	culture volume
c	yield or conversion factor	X	species of bacterium
D	dilution rate	x	concentration of bacterial population in culture medium
k	an "affinity" constant expressing differing abilities of organisms to utilize nutrients at low concentrations	Y	predator organism
M	mean value of ϕ	y	concentration of predator in culture medium (predator population)
P	population density function whose value varies between 0 and 1, depending on concentration of the bacterial population	μ	specific growth rate
S	limiting nutrient	σ	standard deviation of ϕ
s	concentration of limiting nutrient in the culture	ϕ	Gaussian distribution function
s_r	concentration of the nutrient substrate entering the culture (resource)	Subscripts	
		m	maximum
		y	pertaining to predator Y
		1	pertaining to prey bacterial species X
		2	pertaining to competitor bacterial species X

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